COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, X

THE XYLEM OF PERESKIA COLOMBIANA, PERESKIA GUAMACHO, PERESKIA CUBENSIS, AND PERESKIA PORTULACIFOLIA

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OF THE FOUR SPECIES under consideration in this paper the one with the greatest stature is probably *Pereskia colombiana* Britt. & Rose, said to be a tree which attains a height of eleven meters (Backeberg, 1958), but in some localities has a smaller, shrub-like form (Britton & Rose, 1919). The largest section of a stem collected for me by Romero Castañeda, in the type locality of the species in Colombia, is approximately 30 centimeters in diameter.

On the other hand, *Pereskia guamacho* Web. is described as a shrub one to three meters high, but may become a tree ten meters high with a trunk up to 40 centimeters in diameter (Britton & Rose, 1919). The largest stem collected for me by Steyermark in Venezuela is four centimeters in diameter.

Of the other two species considered in this paper, *Pereskia cubensis* Britt. & Rose is commonly a tree up to four meters high (Backeberg, 1958), but under favorable conditions may attain a height of seven meters and a stem diameter of 30 centimeters (Boke, 1954). The largest stem available to me from the Atkins Garden in Cuba is six centimeters in diameter.

The fourth species, *Pereskia portulacifolia* (L.) Haw., is a tree which may attain a height of somewhat more than six meters and stem diameters of as much as 16 centimeters (R. A. Howard, personal communication). The largest stem collected for me by Jiménez at Jimani, Dominican Republic, is four centimeters in diameter.

A number of taxonomists who have studied *Pereskia colombiana* and *P. guamacho* in their native habitats consider them to be conspecific. Therefore, it is desirable to determine whether they are geographical races of a single species or whether their variations in habit of growth and in the form and venation of their leaves are due solely to environmental rather than genetic influences. The structure of the xylem, as of the phloem (Bailey, 1961), and the form and vasculature of the leaves (Bailey, 1960) is remarkably similar in the two putative species. The earlier-formed secondary xylem of stems resembles that of *P. sacharosa* Griseb. and other pereskias discussed in preceding papers of this series. The vessels tend to

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be diffusely distributed in a matrix of dense libriform fibers (FIGS. 1 and 5). The wood parenchyma tends to be scanty paratracheal and the fully lignified multiseriate rays are comparatively narrow. In subsequently formed secondary xylem, there are more or less precocious transitions to a form of structure that does not occur in stems of *P. sacharosa*, *P. grandifolia* Haw., *P. bleo* DC. (Bailey, 1963c) and such pereskias of Peru and Bolivia as *P. humboldtii* Britt. & Rose, *P. weberiana* K. Schum., and *P. diaz-romeroana* Cárd. (Bailey, 1963a), but which appears to be an accentuation of structural changes that occur in the outer secondary xylem of large stems of *P. conzattii* Britt. & Rose, *P. autumnalis* (Eichlam) Rose, and *P. nicoyana* Web. (Bailey, 1963b). The paratracheal parenchyma becomes increasingly abundant forming concentric zones which alternate with zones of greater density, i.e., having fewer vessels and a higher proportion of libriform fibers (FIGS. 2 and 6). The alternating zones vary markedly in width in the transverse section of a large stem, with more or less abrupt transitions from dense to softer tissue (compare FIGS. 2, 3, and 6). Such zonation may prove to be an indication of successive seasonal changes in cambial activity and in the maturation of cambial derivatives.

In stems of *Pereskia colombiana* and *P. guamacho*, as in those of other pereskias, the vessels vary considerably in diameter, in number per unit area, and in their degree of aggregation into clusters and zonal arrangements in different parts of a single mature plant (FIGS. 1–6). The multiseriate rays similarly vary markedly in height, width, form, and spacing; and their constituent cells exhibit conspicuous differences in size, form, and orientation. The most obvious differences occur in passing radially from the first-formed secondary xylem to the outermost wood of enlarged stems. As in other pereskias and in many dicotyledonous trees of normal form, the first-formed multiseriate rays tend to be vertically extensive. During radial extension of these rays they become dissected into lower and wider parts of fusiform outline as seen in tangential longitudinal sections (FIG. 11). These fusiform parts subsequently become laterally displaced during increase in circumference of the cambium (FIGS. 7 and 9). During such transitional changes in the multiseriate rays their successively formed parts exhibit more or less precocious differences in form and orientation of their constituent cells, i.e. from "erect" to nearly isodiametric to "procumbent." At times rays in the outer secondary xylem which are composed largely of slender procumbent cells may be jacketed by broader erect cells (FIG. 7), as in *P. sacharosa* (Bailey, 1962) and *P. conzattii* (Bailey, 1963b).

In the limited number of roots of *Pereskia colombiana* and *P. guamacho* available to me at present, there are more precocious changes in structure than in stems of equivalent diameter. In passing from the first-formed secondary xylem outward, there tends to be an abrupt increase in the diameter of vessels and in their number per unit area, likewise in the amount of paratracheal parenchyma and in the length of procumbent ray cells (FIG. 4). On the contrary, the multiseriate rays tend to retain a vertically extensive form (FIGS. 10 and 12). The inner part of the first-formed multiseriate rays is composed largely of unlignified cells, some of which contain druses and others large single crystals of calcium oxalate. In the outward extension of the rays, patches of unlignified cells alternate with fully lignified parts of the multiseriate rays. Furthermore, more or less extensive arcs of unlignified wood parenchyma occur at times in the roots of these pereskias.

The secondary xylem in stems of *Pereskia cubensis* is of a relatively dense form. The vessels which are diffusely distributed in the inner secondary xylem (FIG. 13) exhibit more or less conspicuous aggregations into concentric patterns in subsequently formed tissue (FIG. 14). The lignified wood parenchyma is scanty paratracheal and the lignified multiseriate rays, which vary considerably in width and in number per unit area, are composed of varying mixtures of slightly erect, isodiametric and slightly procumbent cells (FIGS. 13–15). As in the fully lignified rays in stems of *P. colombiana* and *P. guamacho* crystals of calcium oxalate occur in the form of single large ones or a few independent ones; aggregations into typical druses being absent. The first-formed multiseriate rays are vertically extensive. They become dissected in their outward extension into lower rays of more or less fusiform outline (as seen in tangential longitudinal sections) which become laterally displaced during increase in the circumference of the cambium (FIG. 15). As in other pereskias, in immature stems of largest diameter broadening of the parenchymatous interfascicular gaps of the eustele may occur during later stages of development of the primary body. In such stems (FIG. 13) the innermost part of the first-formed multiseriate rays may be composed of tangentially, rather than vertically or radially, elongated cells. In the outermost secondary xylem of the largest available stem of *P. cubensis* there is no conspicuous occurrence of broad concentric zones of wood parenchyma, such as occur so characteristically in the case of *P. colombiana* and *P. guamacho* in stems of comparable diameters. Unfortunately specimens are not available at present for determining whether such parenchymatous zonations ever occur in the outermost secondary xylem of stems which attain a diameter of 30 centimeters.

The structure of the xylem in roots of *Pereskia cubensis* closely resembles that which occurs in roots of *P. colombiana* and *P. guamacho*. There is a similar tendency for precocious increase in diameter of the vessels, for the occurrence of alternating parts of unlignified and fully lignified cells in the rays, and for the development of more or less extensive arcs of unlignified wood parenchyma (compare FIGS. 4 and 16). Druses as well as single large crystals tend to be present in unlignified parts of the rays. Furthermore, there is a similar tendency for the multiseriate rays to retain a vertically extensive form (compare FIGS. 8, 10, and 12).

The xylem in the largest available stem of *Pereskia portulacifolia* resembles that of *P. cubensis*. The vessels (FIG. 17) are of similar size and distributional patterns, the wood parenchyma is scanty paratracheal and the lignified rays are of comparable variations in form and internal cellular organization (FIGS. 17 and 19). The wood retains its density (i.e. high proportion of libriform fibers) throughout, and even in its outermost part differs conspicuously from that in stems of equivalent diameter of *P. colombiana* and *P. guamacho*, i.e. in the absence of broad concentric zones of wood parenchyma. However, the form and cellular composition of the lignified multiseriate rays in the outermost secondary xylem is fundamentally similar in the four putative species (compare FIGS. 9, 11, and 19).

The xylem in roots of *Pereskia portulacifolia* resembles that which occurs in roots of *P. cubensis, P. guamacho* and *P. colombiana* (FIGS. 18 and 20). In all four of the putative species there is an obvious phylogenetic tendency toward elimination of secondary walls and lignification in parts of the multiseriate rays, and toward the occurrence of more or less numerous and extensive arcs of unlignified wood parenchyma (FIGS. 16, 18, and 20). In the limited number of roots available to me this phylogenetic trend toward increasing succulence appears to be more highly accentuated in roots of *P. cubensis* and *P. portulacifolia* than in those of *P. colombiana* and *P. guamacho*, but such a conclusion needs to be verified by examination of much additional material from many plants of the four species.

CONCLUSIONS

The secondary xylem in stems of *Pereskia cubensis* and *P. portulacifolia* resembles that which occurs in *P. sacharosa, P. grandifolia,* and *P. bleo* in the size and distributional patterns of its vessels, in its density due to a high proportion of libriform fibers, in its scanty paratracheal parenchyma, and in the variations in size and form of its fully lignified multiseriate rays, as well as in the form and orientation of its ray cells in different parts of an adult plant, particularly in passing from the first-formed to the outermost secondary xylem.

The earlier formed secondary xylem in stems of *Pereskia colombiana* and *P. guamacho* resembles the wood of *P. cubensis* and *P. portulacifolia* in its density and grosser anatomical features. But precocious changes to softer (i.e. more succulent) forms of xylem occur in subsequently formed tissue. This arises by formation of relatively broad concentric zones of wood parenchyma and by reduction in the proportion of libriform fibers in the outer secondary xylem as a whole. However, it is in the roots of these four species, as in those of *P. aculeata* and the Andean pereskias, that enhanced succulence is phylogenetically attained by the elimination of secondary walls and lignification in ray cells and wood parenchyma.

The structural similarities in the xylem may be interpreted as an indication that the four taxa are more closely related genetically one to another than they are to other species of *Pereskia*. Furthermore, the very close anatomical similarities in roots and stems of *P. colombiana* and *P. guamacho* strengthen the conclusion of those taxonomists who argue that the two taxa are conspecific.

SUMMARY OF ANATOMICAL EVIDENCE OBTAINED FROM THE PHLOEM AND XYLEM OF VARIOUS TAXA OF THE GENUS PERESKIA

From the point of view of the phylogeny of the dicotyledons as a whole, the leaf-bearing genera, *Pereskia*, *Pereskiopsis* and *Quiabentia* have attained a high level of structural specialization in the cambium and its xylem and phloem derivatives (Bailey & Srivastava, 1962). This is evidenced in the cambium by the much reduced length of fusiform initials and their tendency to occur in stratified or "storied" patterns; *in the xylem*, by short vessel members having simple porous perforation plates, short wood parenchyma strands and septate and non-septate libriform fibers which store starch, and the phylogenetic elimination of uniseriate rays; *in the phloem*, by reduction in length of fusiform parenchyma and parenchyma strands and by the short length and structural modifications of sieve tube members. It should be emphasized in this connection that these salient end-products of evolutionary specialization closely parallel those which occur in trees and woody shrubs of a number of other dicotyledonous families.

Within the genus *Pereskia*, *P. sacharosa* (Bailey, 1962), *P. grandifolia*, and *P. bleo* (Bailey, 1963c) appear to have persisted at this general high level of structural specialization in both stems and roots without conspicuous evidences of special additional trends of evolutionary modification. On the contrary, particularly in the xylem of roots of the Andean pereskias (Bailey, 1963a), *P. colombiana*, *P. guamacho*, *P. cubensis*, and *P. portulacifolia*, and in both roots and stems of *P. aculeata* (Bailey, 1962), there are evidences of a tendency toward increasing succulence due to the elimination of secondary walls and lignification in ray and wood parenchyma. The occurrence of broad zones of lignified wood parenchyma and reduction in the proportion of libriform fibers in the later-formed secondary xylem of stems of *P. colombiana* and *P. guamacho* may likewise possibly be interpreted as additional evidence toward the formation of softer tissue.

In all taxa of *Pereskia* there is a more or less conspicuous tendency in immature stems of largest diameter toward increase in diameter of the parenchymatous interfascicular parts of the eustele and concomitant increase in diameter of the pith during later stages of the development of the primary body of stems. This form of structure leads at times to an increase in width of the inner part of the first-formed multiseriate rays and to modifications in the form and orientation of ray cells. In the case of *P. conzattii*, *P. autumnalis*, and *P. nicoyana* (Bailey, 1963b) this tendency becomes greatly accentuated in the basal parts of the trunks of the trees, where the pith may expand to a diameter of more than six centimeters. The cells in the inner parts of the multiseriate rays remain unlignified and capable of division and transverse enlargement, thus facilitating increase in circumference of the eustele and concomitant expansion of the pith, long after cambial activity is initiated in the fascicular parts of the eustele.

As demonstrated in the second paper of this series (Bailey, 1961), the genus *Pereskia* may be divided anatomically into three distinct categories of taxa upon the basis of consistently stable differences in the form and distribution of sclereids in the secondary phloem. *Pereskia aculeata*, the pereskias of Peru and Bolivia, and those of southern Mexico and Central America belong in one category; *P. sacharosa*, *P. grandifolia*, *P. bleo*, and *P. tampicana* in a second category; and *P. colombiana*, *P. guamacho*, *P. cubensis*, and *P. portulacifolia* in a third category. Within the second and third categories salient structural similarities may be interpreted as indications of relatively close genetic relationships. In the case of the first category salient structural differences raise some question regarding the degrees of genetic relationships between *P. aculeata*, the Andean pereskias, viz. *P. humboldtii*, *P. weberiana*, and *P. diaz-romeroana*, and *P. conzattii*, *P. autumnalis*, and *P. nicoyana* of southern Mexico and Central America.

It should be emphasized in this connection that anatomical details in xylem of pereskias (i.e. in wood which does not exhibit evidence of highly divergent trends of phylogenetic specialization) vary greatly, not only in the same clone when grown under varying environmental influences, but also in different parts of a single mature plant. As previously noted (Bailey & Srivastava, 1962), diagnostic anatomical criteria commonly utilized by wood anatomists in the differentiation of closely related taxa are of questionable reliability in *Pereskia* unless based upon statistical analyses of many specimens from different localities. When such ranges of potential structural variability are taken into consideration in harmony with evidence from salient trends of divergent specialization in rays and wood parenchyma, available data at least suggest that *P. humboldtii*, *P. vargasii* H. Johnson, *P. weberiana*, and *P. diaz-romeroana* may ultimately prove to be geographical variants of a single species. Similarly *P. grandifolia*, *P. bleo*, and *P. tampicana* may ultimately be shown to be conspecific as also *P. pititache* Karw., *P. conzattii*, and *P. autumnalis*, and *P. colombiana* and *P. guamacho*.

The initial stages in *Pereskia* toward elimination of secondary walls and lignification in ray and wood parenchyma, and toward increase in circumference of the eustele and diameter of the pith after cambial activity is initiated in fascicular parts of the primary body, are particularly significant in dealing with the xylem of *Pereskiopsis* and *Quiabentia* which will be discussed in the next paper of this series.

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EXPLANATION OF PLATES

PLATE I

FIGS. 1–4. Transverse sections of the secondary xylem of *Pereskia colombiana* [*Romero*], × 34. 1, First-formed tissue of a large stem. 2, Outer secondary xylem of a large stem. 3, Outer secondary xylem showing increase in wood parenchyma and reduction of libriform fibers. 4, Outer secondary xylem of a large root.

PLATE II

FIGS. 5–8. Transverse and tangential longitudinal sections of secondary xylem. 5, *Pereskia guamacho* [*Steyermark*]. Transverse section of first-formed secondary xylem of a large stem, × 34. 6, *Pereskia guamacho* [*Pittier 12157*]. Transverse section of outer secondary xylem of a large stem, × 34. 7, *The same*, tangential section of the outer secondary xylem, × 43. 8, *Pereskia cubensis* [Atkins Gard.] tangential section of a root, × 43.

PLATE III

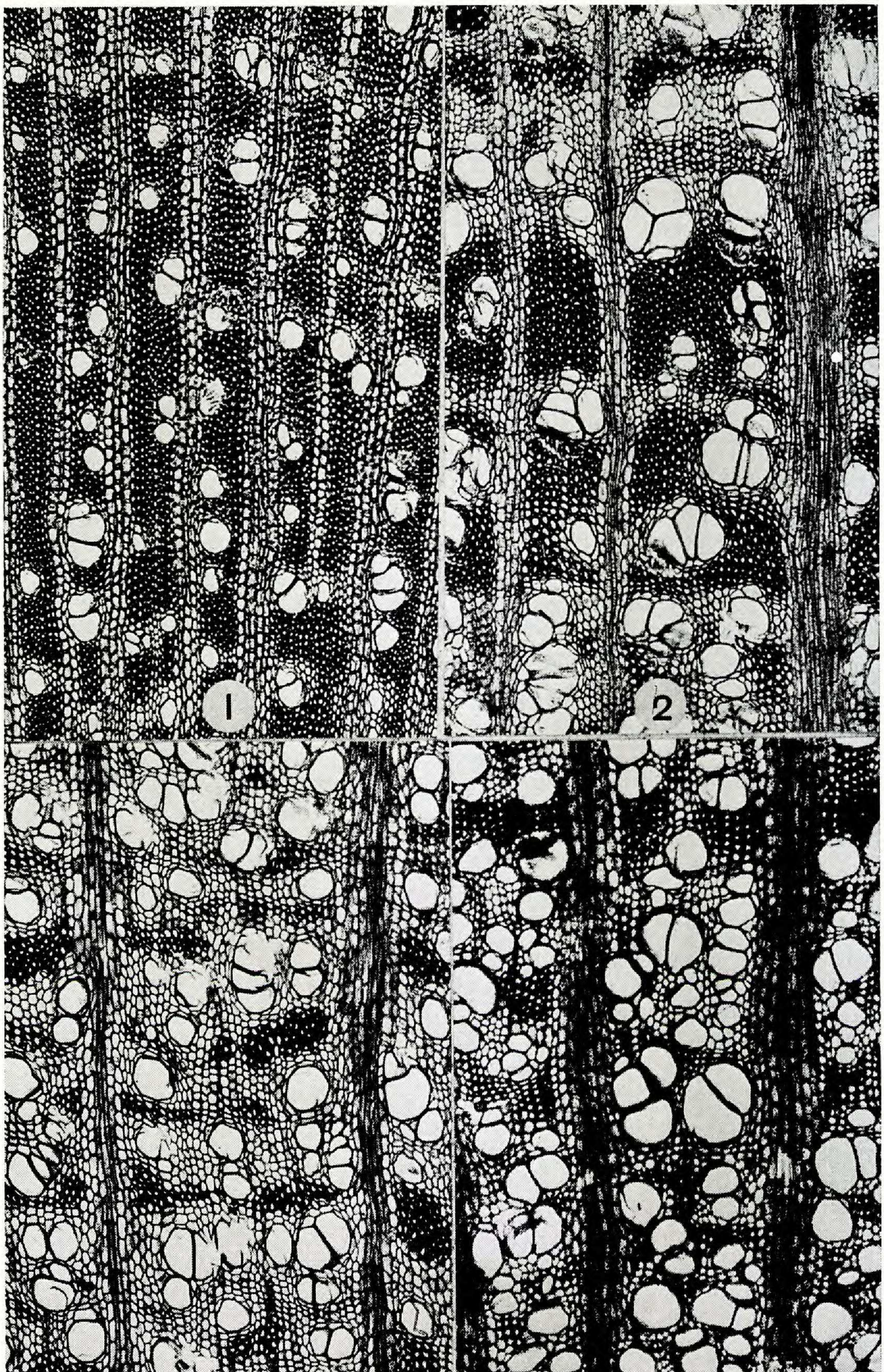
FIGS. 9–12. Tangential longitudinal sections of secondary xylem, × 43. 9, Outer secondary xylem of large stem of *Pereskia colombiana* [*Romero*]. 10, *The same*, root. 11, Outer secondary xylem of large stem of *P. guamacho* [*Steyermark*]. 12, *The same*, root.

PLATE IV

FIGS. 13–16. Transverse and tangential longitudinal sections of the secondary xylem of *Pereskia cubensis* [Atkins Gard.]. 13, Transverse section of innermost secondary xylem of a large stem, × 34. 14, Transverse section of outer secondary xylem, × 11. 15, Tangential section of outer secondary xylem, × 43. 16, Transverse section of root treated with phloroglucin-HCl, showing unlignified parts (white) of multiseriate rays, × 34.

PLATE V

FIGS. 17–20. Transverse and tangential longitudinal sections of the secondary xylem of *Pereskia portulacifolia* [*Jiménez*]. 17, Transverse section of stem, × 11. 18, Transverse section of root, × 11. 19, Tangential section of outer secondary xylem of large stem, × 43. 20, Transverse section of root treated with phloroglucin-HCl, showing unlignified parts (white) of multiseriate rays, × 34.



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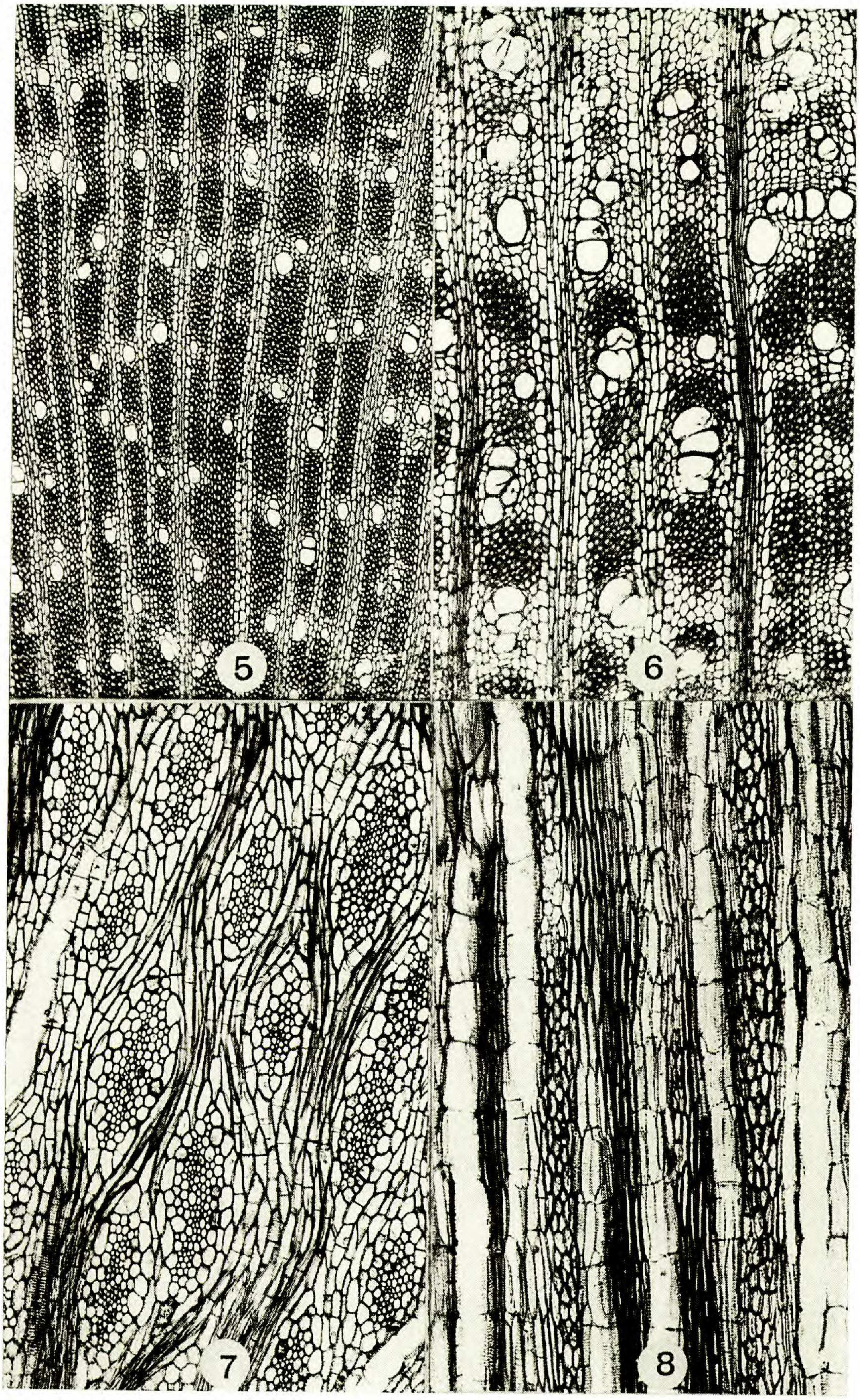

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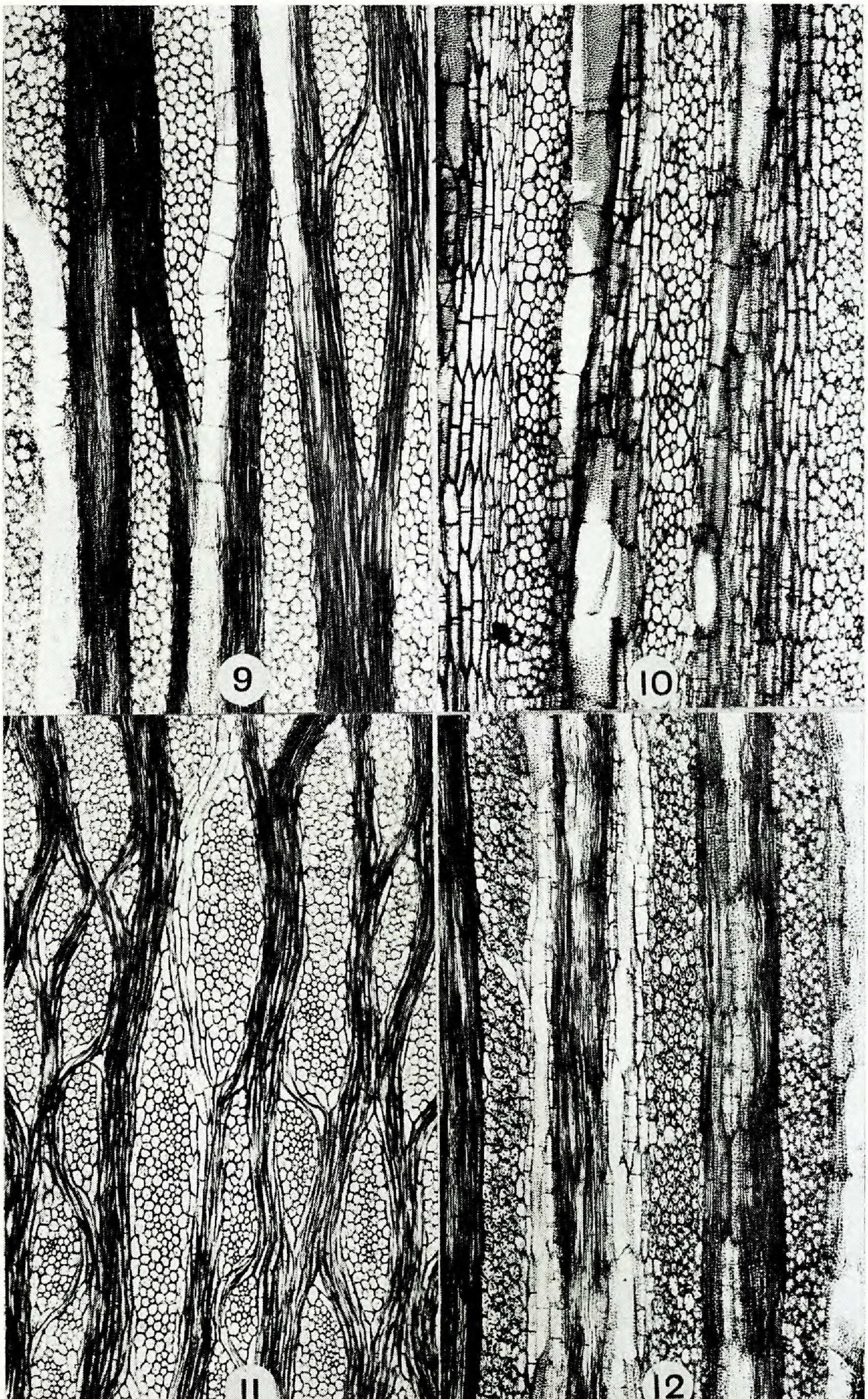

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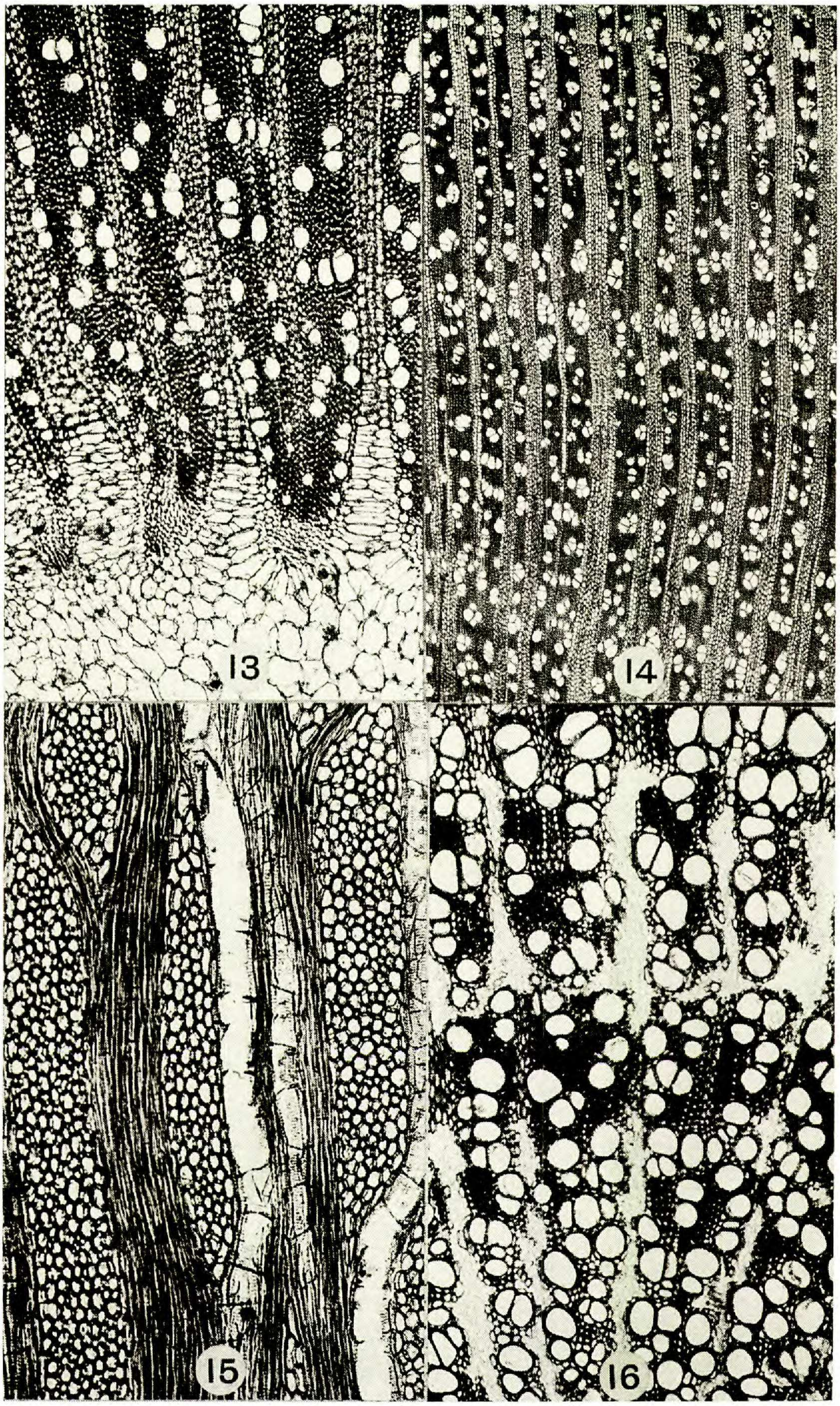

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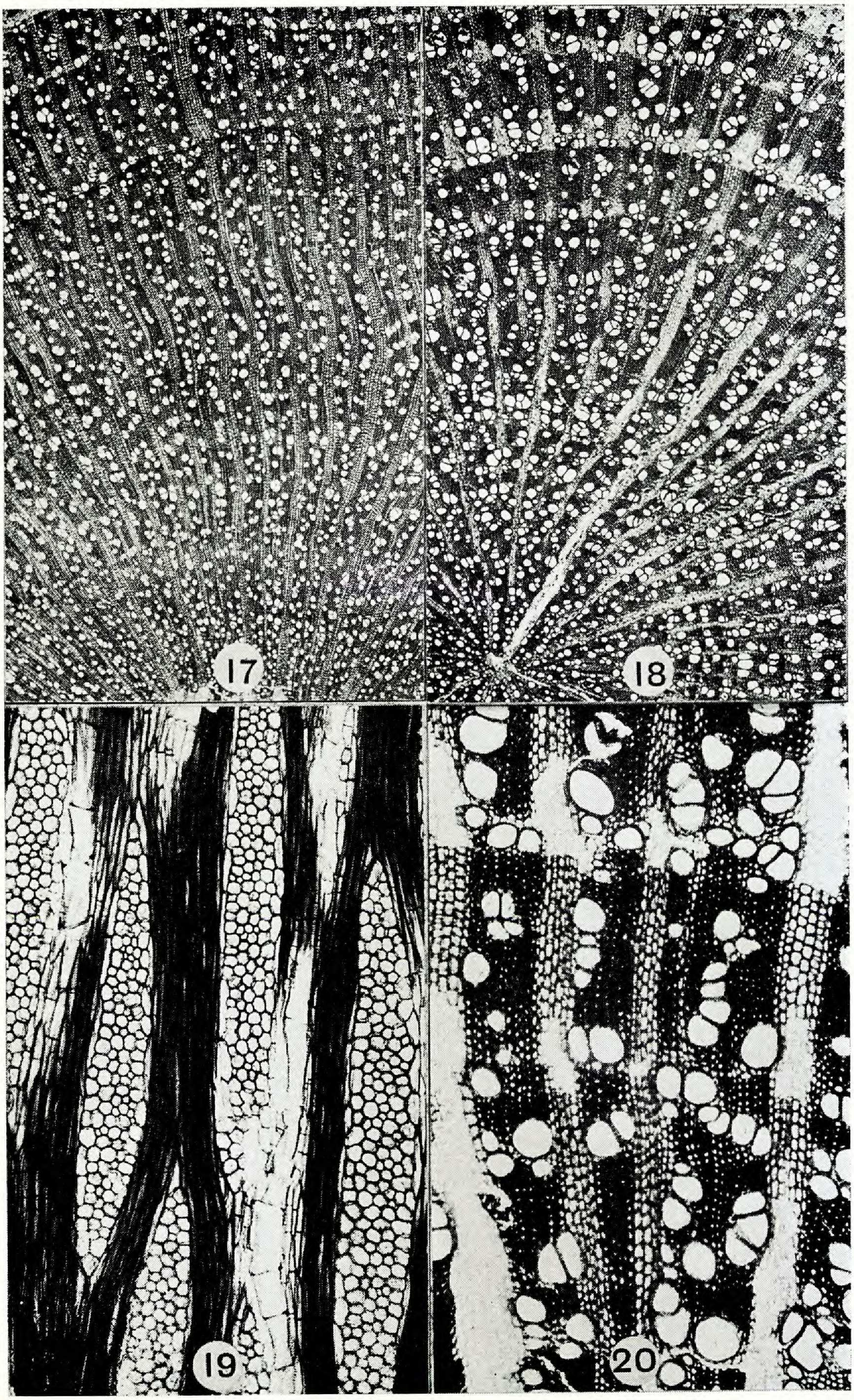

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